

Development and uses of avian skeleton collections

by Storrs L. Olson

SUMMARY

The importance of skeletal material in systematic studies of birds was recognised by only a few nineteenth-century workers yet osteology has been pivotal in the development of phylogenies and classifications of birds and often provides critical clues in problematic cases. In morphometric studies, skeletal material yields far more, and more accurate, measurements and ratios than obtainable from study skins. Skeletons are essential for the identification of fossils, bones from archaeological sites and food items taken by predatory animals, as well as being useful in physiological and histological studies. Although world skeletal inventories have greatly aided researchers, they also reveal serious deficiencies in museum holdings. The need for more material of avian skeletons is undiminished.

Introduction

Systematic studies in the various branches of vertebrate zoology differ fundamentally according to differences in traditional methods of specimen preparation. In cold-blooded vertebrates (fish, amphibians and reptiles) the entire organism is preserved intact in fluid, ultimately usually alcohol, in which colours often change. Thus, in differentiating lower-level taxa there is a heavy emphasis on meristic characters such as number and distribution of spines, fin rays, and especially scales. In birds and mammals the fundamental systematic unit has traditionally been the museum study skin in which the stuffed, dried integument is preserved, with colouration often playing a greater role in systematic decisions than is the case for poikilotherms.

In the preparation of a traditional mammal study skin, only some of the bones of the foot are left in the skin, so that the skinned carcass contains the virtually complete skeleton. Despite this, mammalogists have in the past been scandalously remiss in preserving skeletal material, apart from the skull and mandible, which are saved as part of the skin specimen and which receive equal or greater consideration in systematics. Consequently there is a heavy emphasis on cranial characters, particularly dentition, in mammalogy.

Modern birds, of course, have no dentition, and in the traditional museum study skin most of the skull and bones of the wings, legs and tail are left in the skin. The resulting skinned carcass therefore contains only the bones of most of the vertebral column, pectoral girdle, pelvis and femora, along with all of the viscera, tongue and trachea. After the sex has been determined, this body or trunk carcass is usually discarded. Therefore the process of specimen preparation in ornithology has sometimes been described as peeling off the wrapper and throwing the bird away. Diagnoses of new species and subspecies of birds have been heavily dependent upon plumage colouration and pattern, wing formulae, and the shape and proportions of the wing and tail, so that the ornithologist is far more dependent on feathers than the mammalogist is upon fur.

For a while, the sternum of birds, because it could be easily extracted from the skinned carcass, had a certain vogue as an object of study. Early skeletal collections often contained a high proportion of these sterna, usually with the coracoids and scapulae still attached, and sometimes one may encounter an old skin in collections that still has the sternum tied to the legs or label. Comparative morphology of the sternum occupied the attention of several French ornithologists, and probably reached its zenith with L'Herminier's (1827) classification of birds based on the morphology of the sternum.

Nevertheless, this osteological diversion did little to further the development of avian skeletal collections. The description of new species and subspecies was the principal activity of museum ornithologists during all of the nineteenth and most of the twentieth centuries, and the study skin was the coin of the realm. As traditionally practised, preparation of a complete skeleton meant sacrificing the skin, and field collectors were extremely reluctant to bring back other than well-made study skins, a reluctance that continued through at least to the 1950s. As an example, in his long and distinguished career at the Smithsonian, Alexander Wetmore collected over 27,500 specimens, nearly 14,500 in Panama alone. Despite the fact that Wetmore was active in avian palaeontology, regularly used the Smithsonian skeleton collection, and was instrumental in the Institution's purchase of large and important collections of skeletons, virtually all of the specimens he collected himself were prepared as skins only. The two decades when he was most active in the field marked the period of slowest growth in the Smithsonian skeleton collection in the twentieth century (C. Ludwig, Smithsonian computer files).

History

Serious examination of the avian skeleton can be traced back to the sixteenth century with Belon's (1555) classic comparison of the skeleton of a raven (Fig. 1) with that of *Homo sapiens*. Centuries would pass before the study was taken up again.

Bird skeletons and fluid-preserved specimens were of particular interest to the British ornithologists William Jardine and Thomas Eyton. The correspondence of the celebrated John Gould (Sauer 1998–2001) contains numerous exchanges between these three gentlemen regarding the acquisition of such specimens, and Gould himself took care to obtain anatomical specimens of birds for his colleagues during his own explorations of Australia. Eyton's researches are epitomised by his *Osteologia Avium* (1867–1875).

At the same time in France, Alphonse Milne-Edwards produced his monumental work on the fossil birds of France (1867–1871) in which there are many comparisons with (and illustrations of) the comparative osteology of modern birds. Likewise, skeletal anatomy received considerable attention in his classic work, with Grandidier, on the avifauna of Madagascar, in which the skeletons of many different taxa were illustrated (Milne-Edwards & Grandidier 1876–1881). At least some of Milne-Edwards's collection still exists at the Paris Museum, although I am told that this material was discovered being stored in an alleyway.

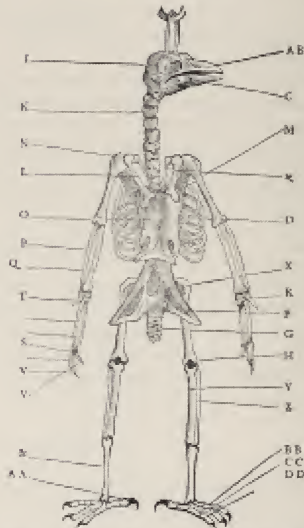
German researchers also investigated the relationships of birds through studies of anatomy, including osteology, which culminated in the exhaustive treatise of Max Fürbringer (1888), whose results were adopted by Hans Gadow (and later Alexander Wetmore) to produce the flawed and derivative—but extremely familiar—system of classification of the orders of birds that dominated ornithological literature throughout the twentieth century.

Comparative anatomy had, of course, long been an important zoological tool and was the subject of intensive research by Baron Cuvier in Paris and later by Richard Owen in England. The field received a tremendous boost after 1859, when Charles Darwin's evolutionary theories provided a rationale for similarities and differences in anatomical structures. The discipline of comparative anatomy was formalised in some museums by the creation of separate departments. The avian skeletal collections in several museums, such as the Smithsonian Institution, Field Museum of Natural History in Chicago, and the Natural History Museum in the U.K., have as their nuclei the specimens inherited from now-defunct departments of comparative anatomy, or from medical museums such as the former museum of the

DES OYSEAVX, PAR P. BELON.
La comparaison de toutes portraits des os humains montre com-
bien celui cy qui est d'un oiseau en est prochain.

4*

Portraits des os de l'oiseau.



A.B. Les os de la tête sont durs et solides, mais ont le bec, comme ceux qui sont en fer, plus ou moins flexibles. Les os qui sont en é. sont en un point et dans le trou.
M. Deux os de la queue qui sont durs et solides.
N. Les os qui sont en fer, et qui sont en fer, et qui sont en fer.
D. Les os de la queue sont durs et solides, mais ont le bec, comme ceux qui sont en fer, plus ou moins flexibles. Les os qui sont en é. sont en un point et dans le trou.
I. Les os de la queue sont durs et solides, mais ont le bec, comme ceux qui sont en fer, plus ou moins flexibles. Les os qui sont en é. sont en un point et dans le trou.
G. Les os de la queue sont durs et solides, mais ont le bec, comme ceux qui sont en fer, plus ou moins flexibles. Les os qui sont en é. sont en un point et dans le trou.
H. Les os de la queue sont durs et solides, mais ont le bec, comme ceux qui sont en fer, plus ou moins flexibles. Les os qui sont en é. sont en un point et dans le trou.
I. Les os de la queue sont durs et solides, mais ont le bec, comme ceux qui sont en fer, plus ou moins flexibles. Les os qui sont en é. sont en un point et dans le trou.
k. Les os de la queue sont durs et solides, mais ont le bec, comme ceux qui sont en fer, plus ou moins flexibles. Les os qui sont en é. sont en un point et dans le trou.

Fig. 1. Skeleton of a Common Raven *Corvus corax*, by Belon (1555). Set next to that of a human skeleton, this was the first detailed illustration of an avian skeleton. © The Natural History Museum, London.

Smithsonian Institution, Field Museum of Natural History in Chicago, and the Natural History Museum in the U.K., have as their nuclei the specimens inherited from now-defunct departments of comparative anatomy, or from medical museums such as the former museum of the

Royal College of Surgeons in Britain and the U.S. Army Medical Museum in Washington.

Uses

Osteology played a pivotal role in the development of phylogenies and classifications of birds, and may still provide critical clues for determining the true relationships of taxa that have long been misplaced. For example, skeletal characters were of paramount importance in showing that the Australian Plainswanderer *Pedionomus torquatus* belongs in the Charadriiformes and not near the Turnicidae in the Gruiformes (Olson & Steadman 1981). Osteological characters were among the many lines of evidence adduced to place flamingos with the Charadriiformes rather than with storks or ducks (Olson & Feduccia 1980). Even single osteological characters, such as fusion of the phalanges of the inner toe in certain genera of Accipitridae (Olson 1982), can provide very suggestive clues as to relationships within a particular group.

Osteology has figured importantly in recent revisionary studies of birds, by using character analyses that supposedly conform with the principles of 'phylogenetic systematics' (e.g. Livezey 1996, 1998), although the results may be viewed as mixed (e.g. Sorensen *et al.* 1999). Prior to this, the rise of phenetics, or numerical taxonomy, in systematics led to a flurry of activity in avian skeletal collections (e.g. Schnell 1970). Although this school waned and phenetics is no longer 'politically correct' in the world of systematics, its temporary ascendancy did result in increased growth of avian skeletal collections and in the emergence of several institutions as major resources of skeletal material. These may not have achieved their present importance had they not had the initial boost provided by the former interest in phenetics.

In the traditional bird study skin, relatively few useful standard measurements can be taken. Furthermore, these measurements can be very difficult to replicate, in part because they may be affected by the state of moult and degree of wear of feathers, or even of wear of the ramphotheca. On the other hand, for morphometric studies the avian skeleton provides many more possible measurements and ratios, which are also much more easily and accurately replicated. Phenetics and morphometrics were certainly factors in the phenomenal growth of the avian skeletal collection at the Royal Ontario Museum, which grew from 1,100 specimens in 1965 to some 48,000 at present (J. Barlow pers. comm.). Large series of skeletons provide a sound basis for assessing geographic size variation within a species. A classic example of this is the study by Rising (1987) of sexual dimorphism in skeletons of Savannah Sparrow *Passerculus sandwichensis*, in which 24 different measurements were taken from 1,791 individuals from 51 populations. For similar studies to be possible, however, much more collecting of specimens would be necessary.

In the investigations mentioned above, the skeletons themselves are the objects of study and the scientific results obtained are taken directly from museum skeletal collections. However, in the most intensive modern use of skeletal collections of

birds, the skeletons, although of critical importance, are secondary and the objects of study are unidentified bird bones that must be compared with skeletons of known identity.

Although it may not be widely appreciated, there are in fact numerous sources of unidentified bird bones. Fossils of all ages are of primary importance for their evolutionary information. In numbers, these would be followed by material from archaeological sites. Skeleton collections are likewise essential for studies of the food remains of predatory birds and mammals; skeletons have been used as indices of body size, and in physiological or histological studies such as those charting changes in bone structure (the Haversian system), or where attempts have been made to age birds using cross sections of long bones.

Other uses of skeletal collections include exhibitions, teaching scientific illustration, other projects which fall into the category of 'art', and various commercial ventures such as use in advertisements. Avian skeletal collections also play an important role in teaching zoology, and, as would be expected, collections associated with universities tend to have had an intensive and consistent use for teaching, whereas other collections tend to have been little used for such purposes. Skeletons are also used to identify birds involved in airplane strikes (although most such identifications are based on feathers), as well as in various forensic applications, such as the identification of carcasses of illegally taken birds or, in rare cases, bird bones that have been taken as evidence in other crimes.

Fossils

In the past quarter century, there has been tremendous growth in the study of fossil birds from all time periods—witness the number of papers, and broad range of subjects, treated in the volumes which emanated from the first four meetings of the Society of Avian Paleontology and Evolution (Mourer-Chauviré 1987, Campbell 1992, Peters 1995, Olson 1999) and two earlier festschrifts (Olson 1976, Campbell 1980). The diagnosis and description of new species is still one of the main activities of avian palaeontologists, and in their work the skeleton has primacy over the study skin. The need for adequate comparative material for identifying fossils has been one of the prime factors in driving the growth of avian skeleton collections. Notable among these are the collection of Pierce Brodkorb (now incorporated in the Florida Museum of Natural History) and those assembled mainly by Evgeny Kurochkin and at the Palaeontological Institute of the Russian Academy of Sciences in Moscow, and by Zygmunt Bochenski at the Polish Academy of Sciences in Krakow.

A good example of how palaeontological studies have spurred the growth of skeletal collections comes from the Caribbean island of Puerto Rico. Alexander Wetmore collected extensively in Puerto Rico and wrote the definitive studies of its avifauna (Wetmore 1916, 1917). Consequently, the Smithsonian collections of Puerto Rican birds were once, for skins, probably the largest and most important in the world. However, when I returned from Puerto Rico in 1976 with tens of thousands of fossil bird bones from cave deposits on the island, I could find only four skeletons,

from three species of bird from Puerto Rico, in the Smithsonian collections. Because this was utterly insufficient for researching the fossil avifaunas, a new campaign of collecting modern comparative material had to be initiated on Puerto Rico and elsewhere in the Antilles. The Smithsonian collections now hold nearly 4,000 skeletons from throughout the West Indies. Well over 90% of these have been collected since 1975, and almost entirely because of their need in palaeontological studies.

The development of modern collections

Although by far the majority of skeletal specimens consist of dry bones in varying degrees of disarticulation, a small number are prepared as cleared and stained specimens in which the soft tissues are rendered more or less translucent and the bones and cartilage are dyed different colours. This essentially involves converting an intact fluid-preserved specimen into a skeletal specimen, although the skeleton is still maintained thereafter in fluid. Cleared and stained specimens have been important in studies of growth and development (Olson 1973, Burke & Feduccia 1997) and in as yet unpublished studies of the systematics of hummingbirds (R. L. Zusi in prep.).

Moreover, it must not be forgotten that, because study skins still contain many of the more diagnostic bones of the avian skeleton, skin collections may become a major source of skeletal material. This is especially useful for extinct species for which no skeletons were ever saved. Methods have been developed where the skull and limb bones can be carefully removed from skins with little or no loss of the scientific value of the study skin itself, yet allowing great gains in knowledge of osteology and even myology (Olson *et al.* 1987). Without such bones extracted from skin collections, the study of the fossil avifauna of the Hawaiian Islands, for example, would have been significantly impeded (James & Olson 1991, Olson & James 1991). Perhaps the best example of the use of this method was the extraction of the skull from the unique holotype of the Lanai Hookbill *Dysmorodrepanis munroi*, after which this was once again classed as a valid genus and species rather than as an aberrant individual of another species (James *et al.* 1989).

Another source of skeletal data from skin specimens is from x-rays, which have been used for determining age in songbirds (Rasmussen 1998) as well as for trying to determine the origins of particular specimens such those of as rare Hawaiian specimens (Olson 1996) or those with fraudulent data (Rasmussen & Collar 1999, Rasmussen & Prÿs-Jones 2003, this volume).

Although specific research projects have added significantly to world holdings of avian skeletons, the growth of skeletal collections has mainly resulted from general collecting in which some of the specimens acquired are chosen for preservation as skeletons. There is now a generally prevalent modern outlook, or ethic, of specimen preparation in museums, that dictates that not all specimens should be made up as study skins and that some balance must be struck between the need for skins, skeletons and fluid-preserved specimens. Concurrent with this shift has been the emergence of an ethic of attempting to obtain maximal information, at least from specimens of

scarcer species. This in turn has given rise to creative new methods of specimen preparation that allow for preservation of skin, skeleton and soft parts in different states of completeness, along with tissue samples for biochemical studies.

Another very positive development has been the appearance of world skeletal inventories (Wood *et al.* 1982, Wood & Schnell 1986), which have provided a great stimulant to the enhancement of skeletal collections. These inventories have provided a rather shocking picture of just how deficient the museum collections of the world are in species represented by non-skin preparations. Field collectors have been able to consult these inventories prior to or during expeditions to determine where gaps in holdings could be filled. Knowing in the field that no osteological material exists for a given species has more than once provided the incentive for preparing a specimen as a skeleton rather than a skin.

Nevertheless, I have detected a few hints of a slight backlash regarding skeletal preparation among those I solicited for information. One collections manager considered that the strong reputation of the skeleton collection at his institution had caused specimens to be prepared as skeletons that should have been made as skins or alcoholics. At another museum, concern was expressed that far less use was being made of the skeleton collection, compared with tissues or skins, which called into question the value of expending so much effort on skeletal preparation. Nevertheless, it is clear that a much healthier balance now exists in most major museums in regard to manner of specimen preparation.

Recognition must be made of the fact that, in North America, increased emphasis on skeletal preparations and the importance of skeletal specimens is in great measure due to the influence of the staff of four museums associated with large universities: Michigan, Kansas, Florida and California (Berkeley). Each of these museums houses large and important collections of bird skeletons and each has a long history of active involvement in avian palaeontology and systematics. There are few ornithologists in North America who regularly use skeletal specimens in their research, or who are now directly responsible for the curation of skeletal collections, who did not receive training at or were not in some other way directly influenced by these four research institutions.

The extent to which individual scientists or collectors have influenced the growth of skeletal collections varies from institution to institution. Some important collections have been formed almost single-handedly, whereas others are the cumulative result of generations of effort by staff, students and associates. Conversely, individual influence has at times slowed collection growth, as when a curator has no interest in studies involving osteology and neither acquires nor prepares skeletal specimens. Archaeological departments in museums and universities, particularly in Europe, have been responsible for developing numerous smaller collections of avian skeletons for use in identifying bone remains from archaeological sites.

Despite these advances, it is a depressing fact that active field collecting of birds is on the wane, being greatly hampered by misplaced sentimentalities and bureaucratic impediments. This comes at a time when there still exist many critical deficiencies

in world museum holdings and when habitats, along with their birds, are being destroyed.

Acknowledgements

For information on the skeletal collections at their institutions I am very grateful to: Jon Barlow (Royal Ontario Museum, Toronto), Jon Fjeldså (Zoological Museum, University of Copenhagen, Denmark), Ned K. Johnson and Carla Cicero (Museum of Vertebrate Zoology, University of California, Berkeley), Mary LeCroy (American Museum of Natural History, New York), Craig Ludwig (National Museum of Natural History, Smithsonian Institution, Washington, D.C.), Robert Prýs-Jones and Don Smith (Natural History Museum, Tring), Mark Robbins (University of Kansas Museum of Natural History, Lawrence), Sievert Rohwer (Burke Museum, University of Washington, Seattle), David W. Steadman (Florida Museum of Natural History, Gainesville), Van Remsen (Museum of Zoology, Louisiana State University, Baton Rouge), and David Willard, (Field Museum of Natural History, Chicago).

Author's note: This essay was developed as a preliminary draft that was intended to be circulated rather widely for comments from curators and users of skeletal collections so that other perspectives might be incorporated. It was first submitted for remarks on format and suggestions that might enable better conformity with other papers in the symposium; but as no more was heard on the subject I did nothing further with it. When it resurfaced three years later, I was asked to allow it to be included, which I have done reluctantly, making only very minor changes. I take no responsibility for the fact that the result is neither current nor particularly well balanced.

References:

- Belon, P. 1555. *L'histoire de la natvre des oyseaux*. Gilles Corrozet, Paris.
- Burke, A. C. & Feduccia, A. 1997. Developmental patterns and the identification of homologies in the avian hand. *Science* 278: 666-668.
- Campbell, K. E., Jr. (ed.) 1980. Papers in avian paleontology honoring Hildegard Howard. *Contrib. Sci. Nat. Hist. Mus. Los Angeles County* 330.
- Campbell, K. E., Jr. (ed.) 1992. Papers in avian paleontology honoring Pierce Brodkorb. *Sci. Ser. Nat. Hist. Mus. Los Angeles County* 36.
- Eyton, T. C. 1858–1867. *Osteologia avium*. R. Hobson, Wellington [with supplements from 1869 to 1875].
- Fürbringer, M. 1888. *Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Stütz- und Bewegungsorgane*. Van Holkema, Amsterdam.
- James H. F. & Olson, S. L. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands. Part II. Passeriformes. *Orn. Monogr.* 46: 1-88.
- James, H. F., Zusi, R. L. & Olson, S. L. 1989. *Dysmorodrepanis munroi* (Fringillidae: Drepanidini), a valid genus and species of Hawaiian Finch. *Wilson Bull.* 101: 159-179.
- L'Herminier, F. J. 1827. Recherches sur l'appareil sternal des oiseaux. *Actes Soc. Linnéenne Paris* 6: 3-93. [Expanded the following year to a separate publication, not seen, reference in Newton (1896:51).]
- Livezey, B. C. 1996. A phylogenetic analysis of geese and swans (Aves: Anserinae), including selected fossil species. *Syst. Biol.* 45: 415-450.
- Livezey, B. C. 1998. A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). *Phil. Trans. R. Soc. London B* 353: 2077-2151.
- Milne-Edwards, A. 1867–1871. *Recherches anatomiques et paleontologiques pour servir a l'histoire des oiseaux fossiles de la France*. Victor Masson, Paris.
- Milne-Edwards, A. & Grandidier, A. 1876–1881. Oiseaux. Vols. 12–15 in Grandidier, A. *Histoire physique, naturelle, et politique de Madagascar*. Impr. Nationale, Paris.
- Mourer-Chauviré, C. (ed.) 1987. L'évolution des oiseaux d'après le témoignage des fossiles. *Doc. Lab. Géologie Lyon* 99: 1-248.
- Newton, A. 1896. *A dictionary of birds*. Adam & Charles Black, London.

- Olson, S. L. 1973. Evolution of the rails of the South Atlantic Islands. *Smithsonian Contrib. Zool.* 152.
- Olson, S. L. (ed.) 1976. Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore. *Smithsonian Contrib. Paleobiol.* 27.
- Olson, S. L. 1982. The distribution of fused phalanges of the inner toe in the Accipitridae. *Bull. Brit. Orn. Cl.* 102: 8-12.
- Olson, S. L. 1996. The contribution of the voyage of HMS *Blonde* (1825) to Hawaiian ornithology. *Arch. Nat. Hist.* 23: 1-42.
- Olson, S. L. (ed.) 1999. Avian paleontology at the close of the 20th century. Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4-7 June 1996. *Smithsonian Contrib. Paleobiol.* 89.
- Olson, S. L., Angle, J. P., Grady, F. V. & James, H. F. 1987. A technique for salvaging anatomical material from study skins of rare or extinct birds. *Auk* 104: 510-512.
- Olson, S. L. & Feduccia, A. 1980. Relationships and evolution of flamingos (Aves: Phoenicopteridae). *Smithsonian Contrib. Zool.* 316.
- Olson, S. L. & James, H. F. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands. Part I. Non-passeriformes. *Orn. Monogr.* 45: 1-88.
- Olson, S. L. & Steadman, D. W. 1981. The relationships of the Pedionomidae (Aves: Charadriiformes). *Smithsonian Contrib. Zool.* 337.
- Peters, D. S. (ed.) 1995. *Acta Palaeornithologica*. 3. Symposium SAPE. 5. Internationale Senckenberg-Konferenz 22.-26. Juni 1992. *Courier Forschungsinstitut Senckenberg* 181.
- Rasmussen, P. C. 1998. Tytler's Leaf Warbler *Phylloscopus tytleri*: non-breeding distribution, morphological discrimination, and ageing. *Forktail* 14: 17-28.
- Rasmussen, P. C. & Collar, N. J. 1999. Major specimen fraud in the Forest Owllet *Heteroglaux* (*Athene* auct.) *blewitti*. *Ibis* 141: 11-21.
- Rasmussen, P. C. & Prýs-Jones, R. 2003. History vs mystery: the reliability of museum specimen data. *Bull. Brit. Orn. Cl.* 123A: 66-94.
- Rising, J. D. 1987. Geographic variation of sexual dimorphism in size of Savannah Sparrows (*Passerculus sandwichensis*): a test of hypotheses. *Evolution* 41: 514-524.
- Sauer, G. C. 1998-2001. *John Gould the bird man: correspondence, with a chronology of his life and works*, 1-4. Maurizio Martino, Mansfield Center, Connecticut.
- Schnell, G. D. 1970. A phenetic study of the suborder Lari (Aves). *Syst. Zool.* 19: 35-57, 264-302.
- Sorenson, M. D., Cooper, A., Paxinos, E. E., Quinn, T. W., James, H. F., Olson, S. L. & Fleischer, R. C. 1999. Relationships of the extinct moa-nalos, flightless Hawaiian waterfowl, based on ancient DNA. *Proc. Roy. Soc. London B* 266: 2187-2193.
- Wetmore, A. 1916. Birds of Porto Rico. *US Dept. Agriculture Bull.* 326: 1-140.
- Wetmore, A. 1917. The birds of Porto Rico and the Virgin Islands. *New York Acad. Sci. Scientific Survey of Porto Rico and the Virgin Islands* 9 (3-4): 245-598.
- Wood, D. S., Zusi, R. L. & Jenkinson, M. A. 1982. *World inventory of avian skeletal specimens 1982*. American Ornithologists' Union & Oklahoma Biological Survey, Norman, Oklahoma.
- Wood, D. S., & Schnell, G. D. 1986. *Revised world inventory of avian skeletal specimens 1986*. American Ornithologists' Union, Norman, Oklahoma.
- Address:* Storrs L. Olson, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.